Author response to editor and reviewer comments for "*The contribution of trees and grasses to productivity of an Australian tropical savanna*" (bg-2015-579).

We thank the Associate Editor and both reviewers for their comments and suggestions about our manuscript. We outline the following as our responses to each of their points.

Reviewer 1

1. *Section 2.2 – Please specify the location of the understory tower relative to the main tower, and also describe how it sits in relation to the canopy openings.*

The understory tower is located 10 m to the west of the main ecosystem tower. Overstory cover at this site is approximately 50 % (Kanniah et al., 2009), so the understory tower was located in a representative spot taking this into consideration. However, we did ensure no large trees were too close to the tower (i.e. <5 m), as these can cause wake turbulence and confound the turbulent fluxes. This explanation is included in section 2.2.

2. *How does the fetch of the understory tower compare to that of the overstory tower? How does the vegetation composition compare between these two fetch areas?*

The fetch of the understory tower is less than that of the main tower. Footprint analysis, using Kljun et al. (2004) in EddyPro v4.1.0 (LI-COR Biosciences, Lincoln, NE) showed that during daytime turbulent conditions, the main tower fetch extended up to 205 (± 9) m, primarily in the west to northwest directions in the wet season and south to southeast directions in the dry season. The understory tower fetch extended up to 44 (± 9) m, primarily in the west and northwest direction in the wet season and east to southeast directions in the dry season. While these two fetch areas do not completely match all the time due to the separation of the two towers, vegetation composition at the site is homogenous when viewed at these spatial scales. This gives us confidence that the understory tower is measuring a representative subset of the ecosystem tower. We explanation has been added to the tower description in section 2.2.

3. *Results- The comparison of wet/dry season fluxes in units of season-1 is confusing if readers don't catch the fact that dry & wet season are each defined as 6 months. It would be helpful to remind readers of this definition at the point where this is presented in the text, and also probably in the figure legends.*

We reiterated in the results section that the units of season^{-1} are defined as 6 months each for the wet and dry season.

4. *p. 19326, lines 1-2: Stem expansion is not a direct indicator of C allocation to woody growth. Stem expansion can be driven far more by water status than by C (Zweifel, 2006). In addition, there is a lag between tree stem expansion and woody biomass production (Cuny et al., 2015). Please modify this statement accordingly.*

   Cuny HE, Rathgeber CBK, Frank D et al. (2015) Woody biomass production lags stemgirth increase by over one month in coniferous forests. Nature Plants, 1, 15160.

   Zweifel R (2006) Intra-annual radial growth and water relations of trees: implications towards a growth mechanism. Journal of Experimental Botany, 57, 1445–1459.

The reviewer raises valid points here and we feel that the wording of our sentence was misleading. While external factors such as water availability and temperature can induce a lag between photosynthetic performance (GPP) and stem growth, particularly in northern hemisphere systems (as shown in the references provided by the reviewer), we do not believe this to be the case for Australian savannas. A-seasonal patterns of water use occur in savanna trees, with increases in dry season sap flow indicating a tree scale response to VPD (O'Grady et al., 1999;Hutley et al., 2000) but with limited leaf water stress (Prior et al., 1997;Prior and Eamus, 2000). To account for this, canopy adjustment via reduction in leaf area helps the trees to manage water stress and maintain GPP through the late dry season (O'Grady et al., 2000;Beringer et al., 2007). Allocation of carbon for starch reserves to replace damaged foliage after regular dry season fires also directs photosynthate away from stem growth (Cernusak et al., 2006;Beringer et al., 2007).

As no further objection was made to our explanation above, we have amended the sentence in question and included the additional paragraph below to further clarify our point.

In addition, stem growth slows and then ceases by the late dry season, therefore GPP measured during this period is likely to be allocated to woody tissue maintenance rather than biomass accumulation (Prior et al., 2004;Cernusak et al., 2006). Allocation of carbon for starch reserves, to replace damaged foliage after regular dry season fires, also directs photosynthate away from stem growth (Cernusak et al., 2006;Beringer et al., 2007). In addition, the dominant eucalypt species also flower and fruit in the dry season, producing a large number of woody capsules (Setterfield and Williams, 1996), which would redirect carbon allocation from biomass accumulation.

Reviewer 2

1. *The paper would benefit from a separate results section and a separate discussion section instead of a combined Result and Discussion section. This section also includes additional methodology (for example page 19321, row 3-8) which decreases clarity. The Result & Discussion section is also very long and includes a lot of numbers which occasionally make the section less readable. Can some of this be replaced/complemented by/with illustrations?*

To address the first point raised by reviewer 2, we have separated the results and discussion section to reduce the size of the section.

For the second point raised, we placed the section identified (page 19321, row 3-8) where it was as we thought that it aided our discussion. We removed part of this section and integrated it into section 2.4 in the methods, where we outline our technique of partitioning NEE. Presentation of the results part of this section was left where it was.

For the third point raised, we felt that the inclusion of numbers in the presentation of our results supported our claims. However, in some cases, these numbers are also referred to in Table 3. We have omitted some of these numbers from the body of the results section (i.e. from the results of respiration and GPP) and directed the reader to Table 3 instead.

2. *Page 19317, row 24-27: "We assumed OR to be the difference between ER and UR". Please provide additional support for this assumption. When the flux of CO2 is from the soil and biosphere to the atmosphere could not then the same CO2 be measure by both sensors?*

Our feedback from reviewer 1 may help clarify this point. The understory tower is measuring a subset of the footprint from that of the main ecosystem tower. Given the homogeneity of the site, we assumed that OR would be the difference between ER and UR. Under turbulent conditions, we are making the assumption that the understory tower is capturing the respiration component from the soil and above ground understory vegetation. Given the ecosystem tower is capturing all respiration components, the subtraction of UR from ER should give us an estimate of the above ground overstory respiration (OR) component. We have amended Page 19317, row 24-27 to include this description to make this point clearer in section 2.4

3. *Page 19326 row 5 says Annual GPP = 2267, wheres table 3 says 2187. A typo?*

Upon double checking Table 3, it seems reviewer 2 may have taken the value of 2187 from the 2013-2014 annual sums section, instead of the mean (+/- SE) section. The mean annual value in Table 3 (last column) gives a value of 2267 for GPP, which is correctly presented on page 19326 row 5. Table 3 has been made clearer by separating the sections so this type of confusion is less likely to occur.

Associate Editor

1. *As referee #2 mentions, the Results and Discussion section is rather long. I agree with this referee that the manuscript could be improved by separating these two sections.*

We have separated the results and discussion sections to reduce the length of the original section.

2. *Comment two of referee #2 regarding partitioning of ER and UR fluxes: Can you please further clarify this point in the manuscript? How is it assured that the measurements at the understorey tower do not include any fluxes originating from the overstorey? Understorey*

and overstorey fluxes seem not separated by internal sublayers, as the ecosystem tower measures both?

We have addressed this point in the manuscript by more clearly identifying that the overstory fluxes we are referring to are the above ground fluxes from the overstory that occur above the height of the understory tower i.e. primarily that of the tree foliage. This assumption holds when turbulent conditions are sufficient to support vertical fluxes. The u* filtering technique removes conditions where this assumption would not hold. The second last paragraph in section 2.4 now reads:

Once respiration was determined, we calculated GPP (as NEE-R). Once a full time series of NEE and GPP and respiration were calculated for both towers, the above ground overstory OR and GPP were calculated by a simple subtraction of understory values from ecosystem values. This technique assumes that, under sufficient turbulent conditions, fluxes measured by the ecosystem tower in excess of the understory tower are fluxes originating from the above ground overstory (i.e. primarily tree foliage). The height of the understory tower ensures that fluxes measured by the tower should only originate from the understory vegetation during turbulent conditions, however a small contribution may occur from overstory stems located within the understory flux footprint.

3. *In addition to above, can you please adjust Figure 6 such that both plots use the same colour bar (i.e. the same colour for same flux values), please replace umol by µmol. Thank you.*

We have replotted Figure 6 to include the correct units and the same colour bar scale for each plot.

References used in responses:

Beringer, J., Hutley, L. B., Tapper, N. J., and Cernusak, L. A.: Savanna fires and their impact on net ecosystem productivity in North Australia, Global Change Biology, 13, 990-1004, 2007.
Cernusak, L. A., Hutley, L. B., Beringer, J., and Tapper, N. J.: Stem and leaf gas exchange and their responses to fire in a north Australian tropical savanna, Plant, Cell and Environment, 29, 632-646, 2006.
Hutley, L. B., O'Grady, A. P., and Eamus, D.: Evapotranspiration from eucalypt open-forest savanna of northern australia, Functional Ecology, 14, 183-194, 2000.
Kanniah, K. D., Beringer, J., Hutley, L. B., Tapper, N. J., and Zhu, X.: Evaluation of Collections 4 and 5 of the MODIS Gross Primary Productivity product and algorithm improvement at a tropical savanna site in northern Australia, Remote Sensing of Environment, 113, 1808-1822, 2009.
Kljun, N., Calanca, P., Rotach, M. W., and Schmid, H. P.: A simple parameterisation for flux footprint predictions, Boundary-Layer Meteorology, 112, 503-523, 2004.
O'Grady, A. P., Eamus, D., and Hutley, L. B.: Transpiration increases during the dry season: Patterns of tree water use in eucalypt open-forests of northern Australia, Tree Physiology, 19, 591-597, 1999.
O'Grady, A. P., Chen, X., Eamus, D., and Hutley, L. B.: Composition, leaf area index and standing biomass of eucalypt open forests near Darwin in the Northern Territory, Australia, Australian Journal of Botany, 48, 629-638, 2000.

Prior, L. D., Eamus, D., and Duff, G. A.: Seasonal and diurnal patterns of carbon assimilation, stomatal conductance and leaf water potential in Eucalyptus tetrodonta saplings in a wet-dry savanna in northern australia, Australian Journal of Botany, 45, 241-258, 1997.
Prior, L. D., and Eamus, D.: Seasonal changes in hydraulic conductance, xylem embolism and leaf area in Eucalyptus tetrodonta and Eucalyptus miniata saplings in a north Australian savanna, Plant, Cell and Environment, 23, 955-965, 2000.
Prior, L. D., Eamus, D., and Bowman, D. M. J. S.: Tree growth rates in north Australian savanna habitats: Seasonal patterns and correlations with leaf attributes, Australian Journal of Botany, 52, 303-314, 2004.
Setterfield, S. A., and Williams, R. J.: Patterns of flowering and seed production in Eucalyptus miniata and E. tetrodonta in a tropical Savanna Woodland, Northern Australia, Australian Journal of Botany, 44, 107-122, 1996.

List of relevant changes made to manuscript

1. Section 2.2 : location of understory tower and description of vegetation homogeneity
2. Section 2.2: Understory tower flux footprint extent within the ecosystem flux footprint
3. Section 2.3: Method used to estimate u* filtering error for the ecosystem tower
4. Section 2.4: Further clarification about how overstory fluxes were estimated
5. Section 3: Now read “Results” only

*Note: changes from here on become difficult to follow in the tracked changed document due to splitting up the results and discussion section.

6. Section 3.2: reminder about definition of season
7. Section 2.3: removal of discussion material and some sentence restructure to make results flow.
8. Section 3.3: removal of numbers listed in Table 3, to reduce confusion. Percentage estimates left instead.
9. Section 3.3: removal of discussion material and some sentence restructure to make results flow.
10. Section 3.4: removal of numbers listed in Table 3, to reduce confusion. Percentage estimates left instead.
11. Section 3.4: removal of discussion material and some sentence restructure to make results flow.
12. Section 3.5: removal of discussion material and some sentence restructure to make results flow.
13. Section 4: Discussion section added
14. Section 4.1: Discussion of NEP results. Some sentence restructure to make section flow.
15. Section 4.2: Discussion of respiration results. Some sentence restructure to make section flow.
16. Section 4.3: Discussion of GPP results. Some sentence restructure to make section flow.
17. Section 4.3: Addition of further explanation in response to reviewer 1 comment 4.
18. Section 4.4: Discussion of inter-annual variability results. Some sentence restructure to make section flow.
19. Section 5: now conclusion section
20. Table 3: now includes vertical divisions between 2012-2013 sums, 2013-2014 sums and Mean (±SE).
21. Figure 6: Amended figure as per editor’s comment 3.

The contribution of trees and grasses to productivity of an Australian tropical savanna.

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Abstract

Savanna ecosystems cover 20 % of the global land surface and account for 25 % of global terrestrial carbon uptake. They support one fifth of the world's human population and are one of the most important ecosystems on our planet. Savanna productivity is a product of the interplay between trees and grass that co-dominate savanna landscapes and are maintained through interactions with climate and disturbance (fire, land use change, herbivory). In this study, we evaluate the temporally dynamic partitioning of overstory and understory carbon dioxide fluxes in Australian tropical savanna using overstory and understory eddy covariance measurements. Over a two year period (September 2012 to October 2014) the overall net ecosystem productivity (NEP) of the savanna was 506.2 (± 22 SE) g C m^{-2} y^{-1}. The total gross primary productivity (GPP) was 2267.1 (± 80 SE) g C m^{-2} y^{-1}, of which the understory contributed 32 %. The understory contribution was strongly seasonal, with most GPP occurring in the wet season (40 % of total ecosystem in the wet season and 18 % in the dry). This study is the first to elucidate the temporal dynamics of savanna understory and overstory carbon flux components explicitly using observational information. Understanding grass productivity is

crucial for evaluating fuel loads, as is tree productivity for quantifying the tree carbon sink. This information will contribute to a significant refinement of the representation of savannas in models, as well as improved understanding of relative tree-grass productivity and competition for resources.

1 Introduction

Savannas are one of the most important ecosystems on our planet due to their vast spatial extent, productivity and rich biodiversity. They are characterised by the coexistence of a discontinuous tree canopy and a more uniformly distributed grassy understory (Scholes and Archer, 1997;House and Hall, 2001;Bond, 2008), and occur in tropical and sub-tropical regions with a strongly seasonal climate. Savannas span 20 % of the global land surface and account for around 25 % of total gross primary production (GPP), making them one of the most important ecosystem sinks of carbon on the planet (Saugier et al., 2001;Grace et al., 2006;Beer et al., 2010;Ryu et al., 2011). This productivity directly translates into biomass accumulation, leading to carbon storage in the tree component and fuel to support herbivory and fire from the grass component. As a result, savannas are an important source of food and income (via grazing) for roughly a quarter of the world’s human population (Scholes and Archer, 1997;Mistry, 2001), as well as an important resource for timber harvesting (Shackleton et al., 2002) and carbon sequestration (Beringer et al., 2007;Kanniah et al., 2011;Lehmann et al., 2014).

Savanna productivity is controlled by wet season duration and growing season length, the annual solar radiation budget, amount and distribution of precipitation, and variation in temperature and cloud cover (Nemani et al., 2003;Kanniah et al., 2010). Arguably, the most important factor limiting productivity is water availability, which has been well documented in the literature over the last 40 years (Scholes and Archer, 1997;House and Hall, 2001;Sankaran et al., 2004;Sankaran et al., 2005;Ma et al., 2007;Garbulsky et al., 2010;Kanniah et al., 2010, 2011). Seasonal moisture variability causes soil water potentials to increase above the plant wilting point at all soil depths during the wet season but fall below wilting point in the dry season (Sarimento, 1996). This has a direct influence on plant lifecycles and savanna productivity. For example, evergreen woody species adopt a phenological strategy where they invest in root systems to access deeper soil moisture stores in order to remain physiologically active for most, if not all, of the year (O'Grady et al., 1999;Hutley et al., 2000). Alternatively, deciduous plants adopt a phenological strategy where they remain dormant through times of water stress as a drought avoidance tactic (Eamus and Prichard, 1998;Eamus, 1999). Grass species typically opt for an annual or perennial phenology as a similar tactic to avoid drought (Andrew and Mott, 1983;Prior et al., 2006;Bond, 2008).

Savannas occupy latitudes close to the equator (between 30 º N and S), so they receive a large amount of solar radiation year round leading to minimal variability in air temperature. Kanniah et al. (2011) showed this to exert little effect on savanna productivity. Yet diffuse radiation is known to penetrate the tree canopy more than direct radiation (Roderick et al., 2001), which should be beneficial to productivity. However, high variability in cloud cover and atmospheric aerosols in the wet and dry season changes the portion of direct and diffuse radiation reaching the land surface (Allen et al., 2008;Kanniah et al., 2013), which has a direct influence on available solar radiation to support productivity. A modelling study from Whitley et al. (2011) suggests savanna productivity can be light limited due to a finite capacity of the vegetation to intercept light given limited canopy cover development. It is clear then that savanna productivity is regulated by a complex interaction of physiological and environmental drivers. The extent to which these drivers influence tree and grass productivity individually has remained largely unexplored (Whitley et al., 2011).

Fire is another fundamental driver of productivity and carbon storage in savannas (Beringer et al., 2007;Bond, 2008;Beringer et al., 2015). High fire frequency and/or fire severity affects plant demographics (hence carbon storage) by reducing tree growth rates and recruitment of juveniles into the mature adult stand (Murphy et al., 2010;Hoffmann et al., 2012;Werner and Prior, 2013). When fire is excluded from savannas, woody thickening and forest encroachment into the savanna boundary can occur (Hoffmann et al., 2012). Scheiter and Higgins (2009) demonstrated this phenomenon using a dynamic global vegetation model where fire was essentially ‘switched off’ in an African savanna, revealing tree dominance increased along with a 13 % rise in biomass. At the global scale, savannas contribute 44% to total biomass fire emissions (Van Der Werf et al., 2010). Therefore, investigating tree-grass productivity dynamics in savannas is ever important for fire management and carbon cycle understanding (Beringer et al., 2015;Scheiter et al., 2015).

In Australia, whilst much is known about the drivers of savanna ecosystem GPP (Beringer et al., 2003;Beringer et al., 2007;Kanniah et al., 2011;Whitley et al., 2011), little is known about the relative contributions of tree and grass productivity, or of their spatial and temporal dynamic (Whitley et al., 2011). Much of the spatial variability in the relative cover fractions of trees and grass is thought to be due to annual rainfall, which defines woody cover and subsequent grass production. The large spatial variation in grass productivity leads to high (1-3 year) fire frequency (Russell-Smith and Yates, 2007;Beringer et al., 2015) that feeds back to control woody plant demographics. Fire typically consumes cured grass biomass, top kills juvenile trees and scorches the bark and leaves of mature canopy trees (Prior et al., 2006;Werner and Franklin, 2010;Werner and Prior, 2013). This in turn changes the savanna productivity balance from a sink to a source of carbon as the tree canopy uses its carbon resources to re-establish lost canopy biomass at a temporary loss of photosynthetic capacity (Beringer et al., 2003;Cernusak et al., 2006;Beringer et al., 2007).

While fire is the most recurrent disturbance in these savannas, wind-storms and cyclones common to this region also cause damage on longer timescales, altering tree-grass productivity (Staben and Evans, 2008;Hutley et al., 2013). Disturbance also arises from biomass grazing of feral buffalo (Werner et al., 2006) and termites (Werner and Prior, 2007;Jamali et al., 2011), which feeds back into the productivity balance of Australian savannas. Taking these disturbances into account, it is estimated that savanna accounts for 33 % of terrestrial carbon stored in Australia (Williams et al., 2004). It is therefore important to understand the partitioning of productivity in these systems in order to understand how they may respond to climatic drivers and future environmental change. Australian savannas provide a great opportunity to do this as they are the most pristine and intact savannas in the world (Mackey et al., 2007).

To understand the consequences of future environmental change for savannas it is important to first understand how the trees and grasses contribute individually to savanna productivity, as well as how they individually and jointly respond to environmental drivers and disturbance. In this paper we use eddy covariance data with the aim to understand the temporal dynamics of tree and grass productivity in an Australian tropical savanna. Two flux towers (understory and overstory), were used to partition GPP between the trees and the grasses for a typical mesic savanna site in northern Australia. Our objectives were to *i)* validate the use of a flux tower in the understory in a savanna, *ii)* estimate the annual net ecosystem production (NEP) of the savanna and partition it into tree and grass contributions; and *iii)* estimate annual overstory and understory GPP and respiration and how they vary seasonally. This research will provide observational information about tree-grass productivity dynamics in an Australian savanna, which will be highly useful for improving and validating model outputs that currently struggle to get savanna dynamics right.

2 Methods

2.1 Site Description

To achieve our aims we utilised data collected at the long-term Howard Springs OzFlux site (-12.4942, 131.15325, http://www.ozflux.org.au/). This site is representative of mesic savanna that occurs in the northern region of Australia, where annual rainfall exceeds 1200 mm. Howard Springs has been the subject of many studies that began in the late 1990's examining patterns of carbon and water flux from the savanna ecosystem (Cook et al., 1998;O'Grady et al., 1999;Hutley et al., 2000;Eamus et al., 2001). These studies prompted the establishment of a permanent tower, which has been used to improve our understanding of how fire affects mass and energy exchange at the ecosystem (Beringer et al., 2003;Beringer et al., 2007) and leaf scale (Cernusak et al., 2006) and on soil greenhouse gas exchanges (Livesley et al., 2011). Howard Springs was later used as a key site in the Savanna Patterns of Energy and Carbon Integrated across the Landscape (SPECIAL) campaign, which looked at variations in savanna carbon, water and energy fluxes down the ecological North Australian Tropical Transect (NATT) (Beringer et al., 2011a;Beringer et al., 2011b). The composition of standing biomass at the site has also been well documented (O'Grady et al., 2000;Hutley et al., 2011) as has the carbon balance and NEP (Chen et al., 2003;Beringer et al., 2007;Kanniah et al., 2009;Kanniah et al., 2011). Howard Springs has also been an important Australian site used as observational input for a number of ecosystem modelling studies (Whitley et al., 2011;Ma et al., 2013;Haverd et al., 2013a). These studies have contributed to our understanding of the soil-land-atmosphere interactions that occur within savannas. Now, a further piece of the puzzle is being added with this study, which will contribute insight into the individual dynamics of tree and grass productivity.

The Howard Springs site is described in detail by Hutley et al. (2013), so only a summary is provided here. Long-term (1941-2014) mean annual rainfall for the Darwin Airport is 1732 (± 44 SE) mm, (Australian Bureau of Meteorology (BoM), station ID: 014015, www.bom.gov.au), which is approximately 20 km from Howard Springs. The majority of this rainfall (85-95 %) occurs within the rainy season from mid-October to mid-April and little to no rainfall occurs during the dry season months from mid-April to September (Cook and

Heerdegen, 2001). This drives a large seasonal contrast in growth, particularly in the understory (Fig. 1). Mean air temperature varies very little from month to month, with a mean daily maximum range of 30.6 to 33.3 ºC and a mean daily minimum range of 19.3 to 25.3 ºC (BoM). Soils are predominantly red Kandosols (Isbell, 1996) that are sandy and loamy, well weathered and nutrient poor. Vegetation is predominantly open forest savanna (Fox et al., 2001;Kanniah et al., 2009), consisting of a woody C3 overstory formed primarily by evergreen *Eucalyptus tetrodonta* (F. Muell.) and *Eucalyptus miniata* (Cunn. Ex Schauer), which are common savanna tree species found across northern Australia (Brooker, 2006). The tree canopy extends to a height of 18 m, with a density of 661 stems ha^{-1} (Hutley et al., 2011). *Erythrophleum chlorostachys* (F. Muell.) and *Terminalia ferdinandiana* (F. Muell) can also be found amongst the dominant overstory species (Hutley et al., 2000;Beringer et al., 2011a). These species drop between 50 to 100 % of their leaves during the dry season (Williams et al., 1997;O'Grady et al., 2000) thereby adding a semi- to fully deciduous component to the overstory.

The understory is comprised mainly of C4 grasses, the bulk biomass consisting of the annual *Sorghum intrans*, with a smaller abundance of the perennial *Heteropogon triticeous* and *S. plumosum. S. intrans* grow 1-3 m in height, depending on light availability, and consists of a single stem (Lazarides et al., 1991;Spangler, 2003), which sets seed in the last few weeks of March each year and persists as a transient seed bank throughout the dry season (Andrew and Mott, 1983). After seeding, the adult plant senesces and cures to form a highly flammable fuel load (i.e. 158 – 426 g dry mass m^{-2} y^{-1} (Beringer et al., 2007), Fig. 1). Also present in the understory are *cycas armstrongii* (cycad) and juvenile overstory species. The understory is highly dynamic due to the boom-bust phenology of the C4 grasses and the competition for resources that exists between these grasses and the other understory species (Fig. 1). Fire is one of the major disturbances in the Howard Springs region, with a recurrence interval of 1-3 years (Russell-Smith and Yates, 2007). Cyclone activity and land use change are other disturbances that are common in the region, but which occur over longer timescales (Hutley et al., 2013).

2.2 Eddy covariance flux measurements

The eddy covariance technique was used at Howard Springs to estimate ecosystem and understory fluxes of carbon and water. Fluxes from the savanna ecosystem tower (overstory and understory combined) were taken from the existing long-term tower (instruments at 21 m) and were supplemented by an understory tower (instruments at 5 m) for a 2 year period from September 2012 to October 2014. The understory tower was located 10 m to the west of the ecosystem tower. Overstory cover at Howard Springs is approximately 50 % (Kanniah et al., 2009), so the understory tower was located in a representative spot taking this into consideration. However, we did ensure no large trees were too close to the tower (i.e. <5 m), as these can cause wake turbulence and confound the turbulent fluxes.

Flux tower instrumentation is described by Beringer et al. (2003), and Hutley et al. (2005) provides further description of eddy covariance theory and data collection in application to savannas (See Table 1 for a full list of tower instrumentation). In summary, both overstory and understory turbulent exchange measurements were carried out using a 3D sonic anemometer (CSAT3, Campbell Scientific, Logan, UT) and an open path infra-red gas analyser (LI-7500, Li-COR Biosciences, Lincoln, NE), which sampled at a rate of 10 Hz with 30 minute block averaging. The gas analyser was remarkably stable but was still re-calibrated every 6-12 months in the lab using NOAA-CMDL gas standards. Soil heat flux and net radiation were measured as per Beringer et al. (2003) and using this we calculated the available energy and the energy balance closure for the ecosystem tower. This provided us with an important initial indicator of systematic error in our flux estimates. Energy balance closure, using daily averaged data to negate the diurnal effects of storage (Leuning et al., 2012) for the ecosystem tower gave a slope of 0.89 and an r^2 of 0.92. We did not attempt to calculate the energy balance closure for the understory tower as it was too difficult to obtain a representative measurement of within-canopy net radiation. Given the average energy balance closure rate for towers across Fluxnet is 0.84 (± 0.2 SE) (Stoy et al., 2013), our ecosystem tower has acceptable energy balance closure and thus gives us one measure of confidence in the use of turbulent fluxes at our site.

To assess the extent of the understory flux tower footprint within that of the ecosystem flux tower, we used the approach of Kljun et al. (2004) implemented in EddyPro v4.1.0 (LI-COR Biosciences, Lincoln, NE). This analysis revealed that during daytime turbulent conditions, the main tower fetch extended up to 205 (± 9) m, primarily in the west to northwest directions in the wet season and south to southest directions in the dry season. The understory tower fetch extended to 44 (± 9) m, primarily in the west and northwest direction in the wet season and east to southeast direction in the dry season. While these two fetch areas do not completely overlap at all times due to the spatial separation of the towers, vegetation composition at the site is homogenous when viewed at these spatial scales. This gives us confidence that the understory tower is measuring a representative subset of the ecosystem tower.

2.3 Data quality assurance and analysis

As we could not determine the energy balance closure for the understory tower, we performed a power spectra and co-spectra analysis to ensure the understory flux measurement system was consistent with known characteristics of turbulent transport (Kaimal and Finnigan, 1994). Use of the eddy covariance technique for measuring turbulent fluxes requires sufficient sampling frequency and duration to ensure the technique captures the complete spectrum of eddies contributing to turbulent transfer and to avoid aliasing (Baldocchi and Meyers, 1991). We analysed 10 Hz data using EddyPro v4.1.0 (Li-COR Biosciences, Lincoln, NE). Normalized ensemble averaged data, binned by frequency, ± 1 hour of solar noon (12:00-14:00), were averaged for five consecutive days in the wet season and dry season (10 hours of data per season) and standard power curves were overlain (Kaimal and Finnigan, 1994).

The importance of standardisation of eddy covariance data processing for inter-annual and inter-site comparison has been encouraged for some time in the flux community (Papale et al., 2006). For this reason, our 30-minute eddy covariance data were quality assured and quality controlled (QA/QC) using the OzFlux standard processing protocol implemented through the OzFluxQC v2.9.4 python scripts, which were developed under creative common licensing by the OzFlux community and can be freely accessed via the OzFlux website (http://www.ozflux.org.au/). Eamus et al. (2013) provided the first summary of the QA/QC processes and corrections involved in the OzFluxQC protocol. In brief, the OzFlux QA/QC process involves making a range test and removal of data spikes, removal of fluxes where more than 1 % of 10 Hz observations are missing from the 30-minute average, linear corrections for sensor drift and calibration changes, and rejection of observations when wind originates from behind the 3D-anemometer and tower. A number of corrections are also applied to the data during the QA/QC process, which include frequency attenuation, 2D coordinate rotation, conversion of sensible heat from virtual to actual flux, application of the WPL correction to account for density effects of heat and water vapour transfer on fluxes (Webb et al., 1980), and correction of soil moisture and soil heat flux measurements.

Once the OzFluxQC checks and corrections were applied, the percentage of carbon flux (NEE), latent heat flux (Fe) and sensible heat flux (Fh) measurements that were either missing or rejected was approximately 11 (± 1 SE) % for the understory tower and 20 (± 1 SE) % for the ecosystem tower. These gaps were filled using a processing package called DINGO (Dynamic INtegrated Gap filling and partitioning for OzFlux, Beringer, unpublished), also developed in Python. This advanced processing technique scans the OzFlux QA/QC'd data and applies a linear interpolation to gaps of < 2 hours. For gaps > 2 hours, DINGO searches for the 10 closest

Australian Bureau of Meteorology (BoM) monitoring sites from a localised database and creates correlations with the flux dataset to find the BoM site with the best correlation and then gap fills using the BoM data. Temperature, humidity, pressure, precipitation and wind speed are all gap filled in this way. Solar radiation is gap filled using gridded satellite radiation and MODIS albedo product (MOD43B3) data. Soil moisture and temperature gaps were filled using the BIOS2 land surface model of the Community Atmosphere Biosphere Land Exchange (CABLE) land surface system (Haverd et al., 2013b;Haverd et al., 2013a), which was driven by 5 km gridded meteorology from the Australian Water Availability Project (AWAP) (Jones et al., 2009). Artificial neural networks (ANN) as described by Beringer et al. (2007) were used to gap fill NEE, Fe, Fh and Fg (soil heat) fluxes.

We also quantified the model and measurement (random only) error components of NEE based on the work of McHugh et al. (this issue). In brief, this technique quantifies measurement error based on a normal distribution of uncertainty, where a daily differencing technique of the critical drivers of NEE identifies where NEE values differ due to random error (Hollinger and Richardson, 2005). Model error was also quantified based on a normal distribution of uncertainty, where actual observations are compared to an equivalently sized gap-filled subsample to identify error in the gap-filling technique (Keith et al., 2009). The combined error estimate is calculated as the quadrature sum of measured and modelled error, assuming independence of the two error estimates.

The u* filtering technique has also been shown to introduce uncertainty in NEP (Papale et al., 2006), so to check this, we re-calculated NEP using the upper ($u*_{upper}$= 0.39) and lower ($u*_{lower}$= 0.24) 95 % confidence intervals for u* from the Ecosystem tower. Using the same error estimation technique, we added the difference between NEP from u*-$u*_{lower}$ and u*-$u*_{upper}$ to the quadrature calculation to account for u* filtering.

2.4 Partitioning NEE

Nocturnal NEE is taken to be equal to respiration and measurements of NEE (and hence respiration) are considered reliable when turbulent transport is sufficient, as defined by a threshold friction velocity (u*) (Goulden et al., 1996). The u* threshold for our site was determined using the DINGO system that implements the approach of Reichstein et al. (2005). This gave a threshold of 0.07 m s^{-1} for the understory and 0.26 m s^{-1} for the ecosystem. Each half hourly value of NEE is checked and if the observed u* falls below the threshold, DINGO removes the NEE value. All valid night-time NEE values were considered as respiration and an ANN was trained to predict respiration with inputs of soil moisture, soil temperature, air temperature and the normalised difference vegetation index (NDVI). Missing values of respiration were gap filled using the predicted values of respiration from the ANN and the predicted values were then extrapolated to the daytime. This process was performed for both tower data sets, which gave us respiration at the ecosystem (ER), understory (UR) and overstory (OR) scales. We assumed OR to be the difference between ER and UR.

Once respiration was determined, we calculated GPP (as NEE-R). Once a full time series of NEE and GPP and respiration were calculated for both towers, overstory OR and GPP were calculated by a simple subtraction of understory values from ecosystem values. ~~For GPP we took the difference between the two towers to be the overstory contribution.~~ This technique assumes that, under sufficient turbulent conditions, fluxes measured by the ecosystem tower in excess of the understory tower are fluxes originating from the above ground overstory (i.e. primarily tree foliage). The height of the understory tower ensures that fluxes measured by the tower should only originate from the understory vegetation during turbulent conditions, however a small contribution may occur from overstory stems located within the understory flux footprint.

We also assessed seasonal patterns of flux components by defining the wet and dry seasons based on Cook and Heerdegen (2001). These authors define each season based on the probability of the occurrence of a 10-day dry period, which we used to define the ‘wet’ season as the six months from 15th October to 15th April (90-95 % of annual rainfall) and the ‘dry’ season as the six months from 16th April to 14th October. We adopted the biological method for dealing with fluxes whereby positive values represent a net sink/uptake of carbon by the savanna and negative values represent a net source/release of carbon from the savanna (Chapin III et al., 2006).

3 Results ~~& Discussion~~

3.1 Validation of the understory tower

Results from the power spectra and co-spectra analysis revealed that the understory flux system at Howard Springs was consistent with expected characteristics of turbulent transfer of CO_2, water and heat as outlined by Kaimal and Finnigan (1994) (Fig. 2). The wet season showed strong turbulent mixing of all three entities, which is evident from their decay rates in the inertial sub-range mirroring that of the ideal decay rate from Kaimal and Finnigan (1994). In contrast, the dry season shows a weaker relationship between turbulence and these components, which is most likely due to the reduced absolute flux magnitudes of CO_2 and water, not from instrumental errors. It is common to see 'messy' co-spectra during periods of minimal flux or under low turbulent conditions (Burba, 2013), so our dry season result is not surprising. Tree canopy cover is 50 % at Howard Springs (Kanniah et al., 2009), so reasonable turbulent mixing within the canopy is likely, particularly during the day. As such, confidence can be placed in the understory fluxes given the moderately open tree canopy (Misson et al., 2007). Further, understory systems have been successfully deployed to make robust within-canopy fluxes in both open and closed canopy ecosystems (Baldocchi and Meyers, 1991;Blanken et al., 1998;Law et al., 1999;Lamaud et al., 2001;Falk et al., 2005;Launiainen et al., 2005;Ma et al., 2007;Misson et al., 2007).

3.2 Net Ecosystem Productivity

Net ecosystem productivity (NEP) was defined as the daily sum of NEE data. Strong seasonality is evident in ecosystem NEP, which tracks variability in rainfall (Fig. 3). The savanna ecosystem remained a sink of carbon most of the annual cycle except for late dry season conditions when it approached a carbon neutral state or was a weak source to the atmosphere (Fig. 3). On a seasonal basis, ecosystem NEP has a larger sink in the wet season, with an average of 325.5 (± 78 SE) g C m^{-2} $season^{-1}$, compared to a lesser sink in the dry season, with an average of 193.7 (± 55 SE) g C m^{-2} $season^{-1}$ (note: seasons are defined as 6 months each). On an annual basis, NEP of the savanna ecosystem over the 2 years was 506.2 (± 22 SE) g C m^{-2} y^{-1}, indicating this mesic savanna was a large net sink of carbon.

~~This figure is slightly higher than previous carbon balance studies at Howard Springs, such as Beringer et al. (2007) who reported a range of 360 to 430 g C m^{-2} y^{-1} using eddy covariance and Chen et al. (2003) who used an inventory and allometric approach to derive a value of 380 g C m^{-2} y^{-1}. A possible reason for this is that the Howard Springs savanna was impacted by cyclone Tracy in the 1970's and is still recovering from the effects, which over time would see an increase in NEP (Hutley et al., 2013).~~

~~The NEP range from Beringer et al. (2007) is fire dependent and highlights the importance of fire as a major driver of productivity in these savannas. At our site, 1-2 weeks before the commencement of this study (August 2012), a moderate intensity wildfire (Table 2) went through the site and resulted in near-complete removal of understory vegetation and large~~

~~overstory scorch (Fig. 1). The savanna ecosystem became a net source of carbon for a number of weeks following the fire before returning to a sink around the onset of the wet season (Fig. 3). The work of Beringer et al. (2007) supports this concept, as they found that the cost of re-establishing lost overstory foliage after a fire event in savanna ecosystems resulted in a shift in savannas from a sink to a source of carbon whilst the overstory was rebuilt. New foliage is not immediately photosynthetically active, so the overstory consumes carbon resources to rebuild its canopy with no assimilation to replace it (Cernusak et al., 2006), hence the shift from sink to source.~~

In contrast to ecosystem NEP, the understory (5 m tower) system measured a net source of carbon to the atmosphere with an annual average of -722.5 (± 14 SE) g C m^{-2} y^{-1} released (Table 3). This is due to the multiple respiration sources captured by the understory flux system that outweigh the photosynthetic uptake of the understory grasses and shrubs. The understory flux system integrates carbon efflux from root respiration (both trees and grasses), shrub, woody re-sprout and grass foliage and stem respiration, plus heterotrophic respiration that occurs below the measurement height (5 m) of the system. This large respiration source outweighs the productivity of the understory grasses resulting in the NEP source measured by the understory system.

~~The seasonality in NEP of these savannas appears to be dependent on the productivity of both the seasonally dynamic C4 understory and the steady input from the shrub and C3 tree overstory. However, due to regularly recurrent fire in these savannas, that consumes understory biomass, the understory grasses contribute minimally to the longer term productivity of these savannas (Hutley and Beringer, 2010;Beringer et al., 2015). Therefore, the increase seen in NEP from the likes of Beringer et al. (2007) and Chen et al. (2003) to our study is mostly due to the growth of the woody overstory.~~

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The NEP figures presented from our research inevitably include a degree of uncertainty due to measurement (random and systematic) and model error. We quantified these errors (Table 4), which revealed that over a given year, combined (random and model) uncertainty in NEP for the ecosystem tower ranged between 27.3 to 36.4 g C m^{-2} y^{-1} (5-7 % of total NEP) and between 33.6 to 43.8 g C m^{-2} y^{-1} for the understory tower (4-6 % of total NEP). ~~The u* filtering technique has also been shown to introduce uncertainty in NEP (Papale et al., 2006), so to check this, we re-calculated NEP using the upper (u*$_{upper}$= 0.39) and lower (u*$_{lower}$= 0.24) 95 % confidence intervals for u* from the Ecosystem tower. Using the same error estimation technique, we~~

~~added the difference between NEP from u*-u*$_{lower}$ and u*-u*$_{upper}$ to the quadrature calculation to account for u* filtering.~~ Estimation of the u* error for the ecosystem tower revealed a range~~This gave a combined model, random and u* error estimate~~ of 25.1 g C m^{-2} y^{-1} for u*$_{lower}$ and 44.0 g C m^{-2} y^{-1} for u*$_{upper}$. Papale et al. (2006) found that NEP uncertainties, with u* accounted for, ranged between 15 to 100 g C m^{-2} y^{-1} for deciduous and evergreen sites in Europe. Given this range, we are confident that the u* filter has performed well as a filter for NEP at our site.

3.3 Partitioning: Respiration

Respiration is a vital component of the carbon balance of ecosystems, being the main process governing the transfer of carbon from an ecosystem back to the atmosphere. Partitioning of the observed NEP into the components of GPP and ER revealed strong seasonality in respiration that closely followed the presence of rainfall (Fig. 4). ~~This trend was most evident at the beginning of the wet season where rainfall would moisten previously dry surface soil layers, thereby initiating soil mineralisation processes, root growth and displacement of CO$_2$ from soil pore spaces (the Birch effect, Birch, 1958). Heterotrophic respiration (HR) is also elevated under moist soil conditions, with the wet season over double the rate of the dry season (i.e. 210 vs 510 g C m^{-2} season^{-1}, Chen et al. (2003)).~~ On an annual basis, savanna ER was -1760.9 (± 58 SE) g C m^{-2} y^{-1} (Table 3). In comparison, UR was -1443.2 (± 18 SE) g C m^{-2} y^{-1}, indicating that ~ 82 % of ER is derived from the understory in these savannas (Fig.4, Table 3). UR dominated the seasonality of ER, going from ~~-479.0 (± 22 SE) g C m^{-2} season^{-1} (net loss from ecosystem) in the dry season to -964.2 (± 40 SE) g C m^{-2} season^{-1} in the wet season, comprising~~ 33 % of annual in the dry season to ~~and~~ 67 % of annual in the wet season (Table 3).~~, respectively, of the annual mean.~~ ~~Soil respiration (SR) is the most dominant element of total ER, and is between 1400 to 1500 g C m^{-2} y^{-1} in these savannas (Chen et al., 2003;Livesley et al., 2011). This explains why estimated UR closely follows the seasonality in ER.~~

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Compared with UR, OR shows much less seasonality, with the dry season contributing ~~-153.7 (± 55 SE) g C m^{-2} season^{-1} (~~48 %~~)~~ and the wet season ~~-156.5 (± 8 SE) g C m^{-2} season^{-1} (~~52 %~~)~~ to the annual sum ~~of -317.7 (± 47 SE) g C m^{-2} y^{-1}~~ (Fig. 4, Table 3). In addition, it also contributes only a small portion (18 %) to ER (Fig. 4, Table 3).

~~We would not expect our OR estimate to be large given that OR is only the contribution of tree leaves and stems to ER and that SR makes up the bulk of ER. This is supported by the work of Chen et al. (2003), who estimated OR at Howard Springs to produce 270 g C m^{-2} y^{-1}. Likewise,~~

~~Cernusak et al. (2006) estimated an annual OR contribution of 275 g C m^{-2} y^{-1}, which was calculated by summing stem and leaf respiration measured *in situ* at the Howard Springs site. These two independent studies both estimated OR within remarkably close range (~15 %) of our tower-derived estimates and give us confidence in our OR estimate, despite the large uncertainties of error from both systems.~~

~~The UR value (1443.2 (± 18 SE) g C m^{-2} y^{-1}) we estimated from the understory tower was a mixed signal of SR and above ground understory respiration (AUR), comprising grasses and woody stems below the height (5 m) of the flux instruments. Chen et al. (2002) monitored soil respiration at Howard Springs using chambers and reported an annual SR rate of 1430 g C m^{-2} y^{-1}. Another study conducted at Howard Springs using soil chambers estimated annual SR as 1211 g C m^{-2} y^{-1} for unburnt plots and 1442 g C m^{-2} y^{-1} for burnt plots (Livesley et al., 2011). Likewise, Richards et al. (2012) reported values of SR in a similar savanna (~40 km from Howard Springs) to range between 770 and 1780 g C m^{-2} y^{-1} for burnt and unburnt plots, respectively. These figures suggest that our estimate of UR from the partitioned flux data is a reasonable estimate. In addition, Chen et al. (2002) reported the wet and dry season components to the annual SR, finding that 71 % of SR occurred in the wet and only 29 % occurred in the dry. These portions are of similar magnitude to those of our study, where the wet season contributed 67 % to annual UR and the dry season 33 %. In our study, UR was at its peak in the wet season, where soil moisture was at its highest, and then fell away to its lowest rate in the late dry season (September-October), where soil moisture was at its lowest. In these savannas, soil moisture is the primary driver of SR with soil temperature being a secondary factor only when volumetric soil moisture is above 5 % (Chen et al., 2003;Richards et al., 2012).~~

~~Whilst the partitioning approach we used provides us with fundamental understanding of how NEE is divided into respiration and GPP, it is important to note that these estimates are subject to inherent uncertainties due to methodological and physical mechanisms. The application of the u* filtering technique can introduce error primarily during the night, when a loss of CO_2 resulting from low turbulence and drainage flows can lead to underestimation of night-time measured NEE, thus respiration (Aubinet, 2008;van Gorsel et al., 2009;Cleverly et al., 2013). An earlier study that used flux partitioning to estimate savanna respiration and GPP reported annual ER rates of 970 g C m^{-2} y^{-1} (Beringer et al., 2007), considerably lower than this study. The two studies are difficult to compare directly due to differences in processing and gap filling techniques for NEE used in each study. The u* threshold value used in the earlier study (0.15~~

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~~m s^{-1}) was determined visually and was fixed at a lower value, causing respiration and GPP to be lower too. The current technique described in this paper for the u* determination is more conservative and results in high respiration and higher GPP (Reichstein et al., 2005). In addition, a considerable archive of data allows for more robust gap filling of data, plus the data periods between the two studies are almost 10 years apart.~~

~~Since the u* threshold technique has its obvious drawbacks, soil chamber measurements of SR, given its fraction of respiration, can provide an independent measurement to verify tower derived respiration. However, chambers incur their own limitations through interference with the objects they measure and encounter issues in up-scaling leading to over- or under-estimation of the true respiration flux (Pumpanen et al., 2004;Keith et al., 2009). Although we did not explicitly use soil chambers alongside the flux towers during this study, the extensive monitoring of SR at Howard Springs (Chen et al., 2002;Livesley et al., 2011) has allowed us to compare our results against independent estimates of SR, which compare well with our values. Given that our tower estimates of respiration obtained from partitioned NEE are consistent within the ranges already published for soil (i.e. Chen et al. (2003);Livesley et al. (2011);Richards et al. (2012)) and overstory (i.e. Chen et al. (2003);Cernusak et al. (2006)) respiration, we are confident that our processing methods have performed well in partitioning NEE into respiration and GPP.~~

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3.4 Partitioning: Gross Primary Productivity

Savanna productivity is strongly influenced by incoming radiation and soil moisture, which are directly linked with precipitation and cloud cover variability in the wet season (Kanniah et al., 2010;Whitley et al., 2011). The wet season is the primary period of productivity in savannas, accounting for 64 % ~~(1440.8 (± 103 SE) g C m^{-2})~~ of annual GPP (Fig. 5, Table 3). In contrast, the dry season contributes only 36 % ~~(826.3 (± 23 SE) g C m^{-2})~~ to annual GPP (Fig. 5, Table 3). This is primarily due to the rapid growth of annual C4 grasses in the understory, which display boom-bust seasonal dynamics. For the duration of this study, the understory contributed 32 % ~~(720.7 (± 18 SE) g C m^{-2} y^{-1})~~ to the total ecosystem uptake via GPP (Fig. 5, Table 3). Of this annual understory GPP contribution, 79 % occurred in the wet season and only 21 % in the dry season. ~~This small dry season contribution to GPP was most likely that of woody re-sprouts and juvenile overstory species, predominantly eucalypts, taking advantage of the senescent grasses to gain biomass in the early dry season (i.e. May-June, Fig. 1) (Prior et al., 2006;Werner, 2012). At the end of the wet season, data from a biomass harvest indicate that~~

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~~these understory woody species make up 23 % of total understory biomass. At Howard Springs, an unusually high density of understory cycads (*Cycas armstrongii*) also flush throughout the dry season, mostly in response to fire or small rainfall events during the early wet season (Watkinson and Powell, 1997), which would also contribute to the observed dry season understory GPP. However, this dry season GPP is small and can be reduced to zero immediately following fire, as was the case at our site in 2013 (Fig. 5). Frequent fires target understory species by consuming fine fuel grassy biomass and suppressing juvenile species. As a consequence, the carbon sequestration potential of these savanna ecosystems is limited, with the removal of 19 to 51 g C m~~$^{-2}$ ~~y~~$^{-1}$ ~~from the ecosystem every year (Beringer et al., 2007;Murphy et al., 2010).~~

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Relative to the understory, seasonal variability of overstory GPP was low and varied from 44 % (dry season) to 53 % (wet season) of annual GPP despite the major shift in surface soil moisture content from the wet to dry season (Fig. 5, Table 3). Large temporal dynamics in overstory GPP were driven not by climate but by fire events (Beringer et al., 2007), where overstory GPP fell close to zero following moderate intensity fire (i.e. September 2012, Table 2), then recovered once overstory reconstruction occurred (i.e. December 2012 (Fig. 5)). Annual GPP at Howard Springs during this study was 2267.1 (± 80 SE) g C m^{-2} y^{-1}, which varied from 1440.8 (± 103 SE) g C m^{-2} season^{-1} in the wet (64 % of annual) to 826.3 (± 23 SE) g C m^{-2} season^{-1} in the dry (36 % of annual). ~~When the overstory is not fire affected, it has a modest inter-annual variability (i.e. ~16 %) in GPP (Beringer et al., 2007), with dry season NEP and evapotranspiration maintained by available moisture sourced from deep soil layers (Cook et al., 1998;O'Grady et al., 1999;Eamus et al., 2002;Kelley et al., 2007). Kelley et al. (2007) used a soil moisture balance technique and sap flow data to infer soil moisture extraction by the overstory to 4.7 m at Howard Springs.~~

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~~Despite the availability of deep soil moisture, there is a slight linear decrease (Fig. 5) evident in overstory GPP from the onset of the dry season to the end that can be attributed to reduced tree leaf area index (LAI). Coinciding with a decrease in LAI is a reduction in leaf stomatal conductance and assimilation rate throughout the dry season as a result of increased atmospheric vapour pressure deficit and soil drying (Duff et al., 1997;Prior et al., 1997), despite overstory transpiration rates remaining relatively unchanged (O'Grady et al. 1999). Although the Howard Springs site is dominated by evergreen eucalypts, these species are known to have fluctuating LAI (1.01 to 0.75) in response to soil drying (Williams et al., 1997;O'Grady et al., 2000). Given that a small portion (i.e. 15%, Hutley et al. (2011)) of the overstory are also semi-~~

~~, brevi- and fully-deciduous species that drop between 50-100 % of their foliage during the dry season (Williams et al., 1997), the observed seasonal variability in GPP is likely a result of the loss of this photosynthetic leaf area (Eamus et al., 2001). In addition, stem growth ceases during the dry season, so GPP measured during the dry season is the result of stem maintenance rather than biomass accumulation (Prior et al., 2004;Cernusak et al., 2006). (Cernusak et al., 2006;Beringer et al., 2007)(Setterfield and Williams, 1996)~~

~~Annual GPP at Howard Springs during this study was 2267.1 (± 80 SE) g C m^{-2} y^{-1}, which varied from 1440.8 (± 103 SE) g C m^{-2} season^{-1} in the wet (64 % of annual) to 826.3 (± 23 SE) g C m^{-2} season^{-1} in the dry (36 % of annual). When compared to the results of Beringer et al. (2007), these numbers are much larger, as is to be expected from our previous discussion of the differences between the two derived GPP and respiration estimates. Our result is also larger than that published by two other studies from Howard Springs that reported annual GPP rates of 1365 g C m^{-2} y^{-1} (Kanniah et al., 2011) and 1475 g C m^{-2} y^{-1} (Whitley et al., 2011). However, these two studies both used the same partitioned data from Beringer et al. (2007). Chen et al. (2003) provide an independent estimate of GPP at the Howard Springs site using an inventory approach based on above and below ground measurements of biomass, and calculated annual GPP as 2080 g C m^{-2} y^{-1}, which is within 8 % of our estimate of GPP. Howard Springs, being relatively close to the coast, was affected by cyclone Tracy in the 1970's and is believed to be still recovering from the impact (Hutley et al., 2013), so we would therefore expect this regrowing site to be a carbon sink. Further research looking back in time at the 12 year flux record for Howard Springs would provide insight into this question, but is beyond the scope of the present study.~~

3.5 Inter-annual variability in savanna fluxes

Although we are only presenting two years of data, these two years ~~had~~ experienced contrasting meteorology. In terms of inter-annual variability, the 2012-2013 wet season had considerably higher NEP than the 2013-2014 wet season (389.8 compared to 235.3 g C m^{-2} season^{-1}, respectively (Fig. 6, Table 3)). We defined our wet and dry seasons as per Cook and Heerdegen (2001), which meant our 'wet' and 'dry' seasons lasted for 6 months each. In 2012-2013, annual rainfall recorded at Howard Springs was 1288 mm, whereas in 2013-2014 it was 1948 mm. Counterintuitively, the corresponding wet season with the lower rainfall total (2012-2013) had a higher GPP of 1543.6 g C m^{-2} season^{-1} compared with only 1337.9 g C m^{-2} season^{-1} in 2013-2014 (Table 3). During this lower rainfall year, solar radiation was greater and resulted in enhanced growing conditions compared to the 2013-2014 wet season (Fig. 7). This suggests that during the wet season, these savannas can experience light limitation to productivity. ~~Whitley et al. (2011), investigating limitations on savanna productivity at annual timescales, drew a similar conclusion. They used the Soil-Plant-Atmosphere (SPA) model (Williams et al., 1996) to investigate the physiological mechanisms responsible for observed carbon and water flux and found that LAI, rather than soil moisture content, was the major driver of savanna GPP. This led Whitley et al. (2011) to conclude that productivity of the mesic savannas in northern Australia is light limited, a conclusion that our wet season data also supports.~~

For the dry seasons, the year with the preceding drier wet season (2012-2013) had a lower net sink of 138.7 compared to 248.6 g C m^{-2} season^{-1} (Fig. 6, Table 3). As annual rainfall was higher for 2013-2014, deep soil moisture storage was also higher for longer in the dry season of 2013-2014 than that for 2012-2013 (Fig. 7). The rate of decrease after the last significant rainfall event of the wet season (i.e. April) also supports this, with the year 2013-2014 equating to a loss rate of 0.6 % per week of soil capacity versus 1.3 % per week for the drier 2012-2013 (Fig. 7). The higher rainfall in 2013-2014 extended the growing season as a result of maintained soil moisture at saturation levels for the beginning of the dry season. ~~Higher water availability would have benefited the overstory, which relies upon deep soil moisture stores to survive the rainless dry season (Eamus et al., 2002;Kelley et al., 2007). Although transpiration rates do not fluctuate significantly from wet to dry season (O'Grady et al., 1999;Hutley et al., 2000), by the late dry season tree productivity is reduced to the point where productivity is used only for maintenance, not growth (Prior et al., 2004). A wetter wet season, resulting in higher soil moisture for longer at deeper layers, would prolong the growing season for the overstory. Myers et al. (1998) found that dry season irrigation resulted in prolonged leaf retention in the early dry season, but by the late dry season, irrigation made no difference to overstory fullness. By the late dry season, soil moisture is at its lowest (Fig. 7). As an adaptation to survive this, the overstory as a whole is also at its lowest canopy cover at this time (Williams et al., 1997;O'Grady et al., 2000).~~

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~~During the dry season, the understory does remain productive (in terms of GPP), which is not due to grass productivity, as these annual species have already senesced. This smaller sink in the understory results from cycads (Watkinson and Powell, 1997) and juvenile overstory species, whose life histories and productivity are tightly linked to fire (as per NEP section) (Murphy et al., 2010;Werner and Franklin, 2010;Werner, 2012). Given that fire frequency in these savannas is every 1-3 years (Russell-Smith and Yates, 2007), it cannot be ignored when considering the temporal dynamics of savanna productivity. Therefore, we argue that whilst~~

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~~light limitation appears to be the primary driver of productivity in the wet season, the inter-annual productivity of these savannas in the dry season appears to be limited by a more complex interaction of water availability for the overstory, particularly in the early dry season, phenology responses of both the understory and overstory to reduced water availability and variability in the occurrence and intensity of fire.~~

4 Discussion

4.1 Net Ecosystem Productivity

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The NEP result found in this study (506.2 (± 22 SE) g C m^{-2} y^{-1}) is slightly higher than previous carbon balance studies at Howard Springs. Beringer et al. (2007) reported a range of 360 to 430 g C m^{-2} y^{-1} using eddy covariance and Chen et al. (2003) used an inventory and allometric approach to derive a value of 380 g C m^{-2} y^{-1}. A possible reason for these differences is that the Howard Springs savanna was impacted by cyclone Tracy in the 1970's and is still recovering from the effects, which over time would see an increase in NEP (Hutley et al., 2013).

The seasonality in NEP of these savannas appears to be dependent on the productivity of both the seasonally dynamic C4 understory and the steady input from the shrub and C3 tree overstory. However, due to regularly recurrent fire in these savannas, that consumes understory biomass, the understory grasses contribute minimally to the longer term productivity of these savannas (Hutley and Beringer, 2010;Beringer et al., 2015). Therefore, the increase seen in NEP from the likes of Beringer et al. (2007) and Chen et al. (2003) to our study is mostly due to the growth of the woody overstory.

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The NEP range from Beringer et al. (2007) is fire dependent and highlights the importance of fire as a major driver of productivity in these savannas. At our site, 1-2 weeks before the commencement of this study (August 2012), a moderate intensity wildfire (Table 2) went through the site and resulted in near-complete removal of understory vegetation and large overstory scorch (Fig. 1). The savanna ecosystem became a net source of carbon for a number of weeks following the fire before returning to a sink around the onset of the wet season (Fig. 3). The work of Beringer et al. (2007) supports this concept, as they found that the cost of re-establishing lost overstory foliage after a fire event in savanna ecosystems resulted in a shift in savannas from a sink to a source of carbon whilst the overstory was rebuilt. New foliage is not immediately photosynthetically active, so the overstory consumes carbon resources to rebuild its canopy with no assimilation to replace it (Cernusak et al., 2006), hence the shift from sink to source.

~~This figure is slightly higher than previous carbon balance studies at Howard Springs, such as Beringer et al. (2007) who reported a range of 360 to 430 g C m^{-2} y^{-1} using eddy covariance and Chen et al. (2003) who used an inventory and allometric approach to derive a value of 380 g C m^{-2} y^{-1}. A possible reason for this is that the Howard Springs savanna was impacted by cyclone Tracy in the 1970's and is still recovering from the effects, which over time would see an increase in NEP (Hutley et al., 2013).~~

4.2 Respiration

One of the most striking results from our partitioning analysis was the domination of respiration in the understory, which rendered the NEP of the understory as an annual source of carbon to the atmosphere (Fig. 3). The UR value (1443.2 (± 18 SE) g C m^{-2} y^{-1}) we estimated from the understory tower was a mixed signal of SR and above ground understory respiration (AUR), comprising grasses and woody stems below the height (5 m) of the flux instruments. Chen et al. (2002) monitored soil respiration at Howard Springs using chambers and reported an annual SR rate of 1430 g C m^{-2} y^{-1}. Another study conducted at Howard Springs using soil chambers estimated annual SR as 1211 g C m^{-2} y^{-1} for unburnt plots and 1442 g C m^{-2} y^{-1} for burnt plots (Livesley et al., 2011). Likewise, Richards et al. (2012) reported values of SR in a similar savanna (~40 km from Howard Springs) to range between 770 and 1780 g C m^{-2} y^{-1} for burnt and unburnt plots, respectively. These figures suggest that our estimate of UR from the partitioned flux data is a reasonable estimate.

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To further support our UR results, Chen et al. (2002) reported the wet and dry season components to the annual SR, finding that 71 % of SR occurred in the wet and only 29 % occurred in the dry. These portions are of similar magnitude to those of our study, where the wet season contributed 67 % to annual UR and the dry season 33 %. In our study, UR was at its peak in the wet season, where soil moisture was at its highest, and then fell away to its lowest rate in the late dry season (September-October), where soil moisture was at its lowest. In these savannas, soil moisture is the primary driver of SR with soil temperature being a secondary factor only when volumetric soil moisture is above 5 % (Chen et al., 2003;Richards et al., 2012). This trend was most evident at the beginning of the wet season where rainfall would moisten previously dry surface soil layers, thereby initiating soil mineralisation processes, root growth and displacement of CO_2 from soil pore spaces (the Birch effect, Birch, 1958). Heterotrophic respiration (HR) is also elevated under moist soil conditions, with the wet season over double the rate of the dry season (i.e. 210 vs 510 g C m^{-2} season^{-1}, Chen et al.

(2003)).~~Soil respiration (SR) is the most dominant element of total ER, and is between 1400 to 1500 g C m^{-2} y^{-1} in these savannas (Chen et al., 2003;Livesley et al., 2011). This explains why estimated UR closely follows the seasonality in ER.~~

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In contrast to UR, OR did not vary as much over the course of the study period and remained only a small fraction of ER over time (Fig. 4). We would not expect our OR estimate to be large given that OR is only the contribution of tree leaves and stems to ER and that SR makes up the bulk of ER. This is supported by the work of Chen et al. (2003), who estimated OR at Howard Springs to produce 270 g C m^{-2} y^{-1}. Likewise, Cernusak et al. (2006) estimated an annual OR contribution of 275 g C m^{-2} y^{-1}, which was calculated by summing stem and leaf respiration measured *in situ* at the Howard Springs site. These two independent studies both estimated OR within remarkably close range (~15 %) of our tower-derived estimate of -317.7 (± 47 SE) g C m^{-2} y^{-1},~~s and~~ give~~e~~ing us confidence in our OR estimate, despite the large uncertainties of error from both systems.

~~The UR value (1443.2 (± 18 SE) g C m^{-2} y^{-1}) we estimated from the understory tower was a mixed signal of SR and above ground understory respiration (AUR), comprising grasses and woody stems below the height (5 m) of the flux instruments. Chen et al. (2002) monitored soil respiration at Howard Springs using chambers and reported an annual SR rate of 1430 g C m^{-2} y^{-1}. Another study conducted at Howard Springs using soil chambers estimated annual SR as 1211 g C m^{-2} y^{-1} for unburnt plots and 1442 g C m^{-2} y^{-1} for burnt plots (Livesley et al., 2011). Likewise, Richards et al. (2012) reported values of SR in a similar savanna (~40 km from Howard Springs) to range between 770 and 1780 g C m^{-2} y^{-1} for burnt and unburnt plots, respectively. These figures suggest that our estimate of UR from the partitioned flux data is a reasonable estimate. In addition, Chen et al. (2002) reported the wet and dry season components to the annual SR, finding that 71 % of SR occurred in the wet and only 29 % occurred in the dry. These portions are of similar magnitude to those of our study, where the wet season contributed 67 % to annual UR and the dry season 33 %. In our study, UR was at its peak in the wet season, where soil moisture was at its highest, and then fell away to its lowest rate in the late dry season (September-October), where soil moisture was at its lowest. In these savannas, soil moisture is the primary driver of SR with soil temperature being a secondary factor only when volumetric soil moisture is above 5 % (Chen et al., 2003;Richards et al., 2012).~~

Whilst the partitioning approach we used provides us with fundamental understanding of how NEE is divided into respiration and GPP, it is important to note that these estimates are subject to inherent uncertainties due to methodological and physical mechanisms. The application of the u* filtering technique can introduce error primarily during the night, when a loss of CO_2 resulting from low turbulence and drainage flows can lead to underestimation of night time measured NEE, thus respiration (Aubinet, 2008;van Gorsel et al., 2009;Cleverly et al., 2013). An earlier study that used flux partitioning to estimate savanna respiration and GPP reported annual ER rates of 970 g C m^{-2} y^{-1} (Beringer et al., 2007), considerably lower than this study. The two studies are difficult to compare directly due to differences in processing and gap filling techniques for NEE used in each study. The u* threshold value used in the earlier study (0.15 m s^{-1}) was determined visually and was fixed at a lower value, causing respiration and GPP to be lower too. The current technique described in this paper for the u* determination is more conservative and results in high respiration and higher GPP (Reichstein et al., 2005). In addition, a considerable archive of data allows for more robust gap filling of data, plus the data periods between the two studies are almost 10 years apart.

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Since the u* threshold technique has its obvious drawbacks, soil chamber measurements of SR, given its fraction of respiration, can provide an independent measurement to verify tower derived respiration. However, chambers incur their own limitations through interference with the objects they measure and encounter issues in up-scaling leading to over- or under-estimation of the true respiration flux (Pumpanen et al., 2004;Keith et al., 2009). Although we did not explicitly use soil chambers alongside the flux towers during this study, the extensive monitoring of SR at Howard Springs (Chen et al., 2002;Livesley et al., 2011) has allowed us to compare our results against independent estimates of SR, which compare well with our values. Given that our tower estimates of respiration obtained from partitioned NEE are consistent within the ranges already published for soil (i.e. Chen et al. (2003);Livesley et al. (2011);Richards et al. (2012)) and overstory (i.e. Chen et al. (2003);Cernusak et al. (2006)) respiration, we are confident that our processing methods have performed well in partitioning NEE into respiration and GPP.

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4.3 Gross Primary Productivity

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GPP was highly seasonal at Howard Springs, which was largely driven by the difference in understory productivity from wet to dry season (Fig. 6). This is mostly due to the dominating

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presence of C4 grasses in the understory that are primarily active in the wet season (Andrew and Mott, 1983;Whitley et al., 2011). Despite this, understory GPP did not fully cease in the dry season. This small dry season contribution to GPP was most likely that of woody re-sprouts and juvenile overstory species, predominantly eucalypts, taking advantage of the senescent grasses to gain biomass in the early dry season (i.e. May-June, Fig. 1) (Prior et al., 2006;Werner, 2012). At the end of the wet season, data from a biomass harvest indicate that these understory woody species make up 23 % of total understory biomass.

At Howard Springs, an unusually high density of understory cycads (*Cycas armstrongii*) also flush throughout the dry season, mostly in response to fire or small rainfall events during the early wet season (Watkinson and Powell, 1997),. These ~~which~~ would also contribute to the observed dry season understory GPP. However, this dry season GPP is small and can be reduced to zero immediately following fire, as was the case at our site in 2013 (Fig. 5). Frequent fires target understory species by consuming fine fuel grassy biomass and suppressing juvenile species. As a consequence, the carbon sequestration potential of these savanna ecosystems is limited, with the removal of 19 to 51 g C m^{-2} y^{-1} from the ecosystem every year (Beringer et al., 2007;Murphy et al., 2010).

Overstory GPP was less variable over the course of the study than understory GPP and was affected by fire on a number of occasions (Fig. 5, Table 3). ~~When~~Past work at Howard Springs has shown that when the overstory is not fire affected, it has a modest inter-annual variability (i.e. ~16 %) in GPP (Beringer et al., 2007), with dry season NEP and evapotranspiration maintained by available moisture sourced from deep soil layers (Cook et al., 1998;O'Grady et al., 1999;Eamus et al., 2002;Kelley et al., 2007). Kelley et al. (2007) used a soil moisture balance technique and sap flow data to infer soil moisture extraction by the overstory to 4.7 m at Howard Springs.

Despite the availability of deep soil moisture, there is a slight linear decrease (Fig. 5) evident in overstory GPP from the onset of the dry season to the end that can be attributed to reduced tree leaf area index (LAI). Coinciding with a decrease in LAI is a reduction in leaf stomatal conductance and assimilation rate throughout the dry season as a result of increased atmospheric vapour pressure deficit and soil drying (Duff et al., 1997;Prior et al., 1997), despite overstory transpiration rates remaining relatively unchanged (O'Grady et al. 1999). Although the Howard Springs site is dominated by evergreen eucalypts, these species are known to have fluctuating LAI (1.01 to 0.75) in response to soil drying (Williams et al., 1997;O'Grady et al.,

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2000). Given that a small portion (i.e. 15%, Hutley et al. (2011)) of the overstory are also semi-, brevi- and fully-deciduous species that drop between 50-100 % of their foliage during the dry season (Williams et al., 1997), the observed seasonal variability in GPP is likely a result of the loss of this photosynthetic leaf area (Eamus et al., 2001).

In addition to the loss of leaf area, stem growth slows and then ceases by the late dry season. Therefore, GPP occurring during this period is likely to be allocated to woody tissue maintenance rather than biomass accumulation (Prior et al., 2004;Cernusak et al., 2006). Allocation of carbon for starch reserves, to replace damaged foliage after regular dry season fires, also directs photosynthate away from stem growth (Cernusak et al., 2006;Beringer et al., 2007). The dominant eucalypt species also flower and fruit in the dry season, producing a large number of woody capsules (Setterfield and Williams, 1996), which would redirect carbon allocation from biomass accumulation.

At the ecosystem scale, our estimate of annual GPP (2267.1 (± 80 SE) g C m^{-2} y^{-1}) was larger w~~W~~hen compared to the results of Beringer et al. (2007).~~, these numbers are much larger, as~~This is to be expected from our previous discussion in section 4.2 of the differences between the two derived GPP and respiration estimates. Our result is also larger than that published by two other studies from Howard Springs that reported annual GPP rates of 1365 g C m^{-2} y^{-1} (Kanniah et al., 2011) and 1475 g C m^{-2} y^{-1} (Whitley et al., 2011). However, these two studies both used the same partitioned data from Beringer et al. (2007). Chen et al. (2003) provide an independent estimate of GPP at the Howard Springs site using an inventory approach based on above and below ground measurements of biomass, and calculated annual GPP as 2080 g C m^{-2} y^{-1}, which is within 8 % of our estimate of GPP. Howard Springs, being relatively close to the coast, was affected by cyclone Tracy in the 1970's and is believed to be still recovering from the impact (Hutley et al., 2013), so we would therefore expect this regrowing site to be a carbon sink. Further research looking back in time at the 15 year flux record for Howard Springs would provide insight into this question, but is beyond the scope of the present study.

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4.4 Inter-annual variability in savanna fluxes

~~Whitley et al. (2011), investigating limitations on savanna productivity at annual timescales, drew a similar conclusion. They used the Soil-Plant-Atmosphere (SPA) model (Williams et al., 1996) to investigate the physiological mechanisms responsible for observed carbon and water flux and found that LAI, rather than soil moisture content, was the major driver of savanna GPP. This led Whitley et al. (2011) to conclude that productivity of the mesic~~

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~~savannas in northern Australia is light limited, a conclusion that our wet season data also supports.~~

Our comparison of the two meteorologically contrasting years at Howard Springs implies that GPP in these savannas is light limited. Whitley et al. (2011), investigating limitations on savanna productivity at annual timescales, drew a similar conclusion. They used the Soil-Plant-Atmosphere (SPA) model (Williams et al., 1996) to investigate the physiological mechanisms responsible for observed carbon and water flux and found that LAI, rather than soil moisture content, was the major driver of savanna GPP. This led Whitley et al. (2011) to conclude that productivity of the mesic savannas in northern Australia is light limited, a conclusion that our wet season data also supports.

In contrast, our data suggests that the dry season following a wetter wet season results in higher GPP (Fig. 6, Table 2). A wetter wet season provides a greater recharge of soil moisture stores (Fig. 7), which ~~Higher water availability~~ would ~~have~~ benefit~~ed~~ the overstory, ~~which~~as it relies upon deep soil moisture stores to survive the rainless dry season (Eamus et al., 2002;Kelley et al., 2007). Although transpiration rates do not fluctuate significantly from wet to dry season (O'Grady et al., 1999;Hutley et al., 2000), by the late dry season tree productivity is reduced to the point where productivity is used only for maintenance, not growth (Prior et al., 2004). A wetter wet season, resulting in higher soil moisture for longer at deeper layers, would prolong the growing season for the overstory. Myers et al. (1998) found that dry season irrigation resulted in prolonged leaf retention in the early dry season, but by the late dry season, irrigation made no difference to overstory fullness. By the late dry season, soil moisture is at its lowest (Fig. 7). As an adaptation to survive this, the overstory as a whole is also at its lowest canopy cover at this time (Williams et al., 1997;O'Grady et al., 2000).

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During the dry season, the understory does remain productive (in terms of GPP), which is not due to grass productivity, as these annual species have already senesced. This smaller sink in the understory results from cycads (Watkinson and Powell, 1997) and juvenile overstory species, whose life histories and productivity are tightly linked to fire (as per NEP section) (Murphy et al., 2010;Werner and Franklin, 2010;Werner, 2012). Given that fire frequency in these savannas is every 1-3 years (Russell-Smith and Yates, 2007), it cannot be ignored when considering the temporal dynamics of savanna productivity. Therefore, we argue that whilst light limitation appears to be the primary driver of productivity in the wet season, the inter-

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annual productivity of these savannas in the dry season appears to be limited by a more complex interaction of water availability for the overstory, particularly in the early dry season, phenology responses of both the understory and overstory to reduced water availability and variability in the occurrence and intensity of fire.

45 Conclusion

We have described the importance of the complex tree-grass relationship for regulating the dynamics of the carbon balance of a tropical savanna in northern Australia. The understory dominated the wet season GPP component as the rapid growth of the C4 grasses swiftly converts atmospheric carbon into biomass. However, due to the sudden senescence of these C4 grasses at the onset of the dry season, the understory contributes less than the overstory to annual ecosystem GPP. The strength and duration of the wet season monsoon also played a key role in the productivity of these savannas, with the drier year leading to higher understory productivity, and wetter year providing higher soil moisture stores to support overstory productivity for longer during the dry season. This has important implications for the carbon balance of these savannas in light of future climate change, where altered monsoon regimes are likely to vary annual rainfall totals. Since understory productivity transfers directly into biomass that makes up the dominant fire fuel load in these savannas, if the monsoon becomes weaker it could result in years of greater fire intensity due to the higher fuel load in the understory. This in turn could result in a loss of carbon sequestration and reduced biodiversity in savannas (Scheiter et al., 2015). If the monsoon is to strengthen, the overstory will likely be at a productive advantage over the grasses, which in turn could lead to woody encroachment and a shift in biodiversity (Scheiter et al., 2015). Our research has shown that flux towers can be successfully administered in savanna ecosystems to provide a robust observation-based account of tree and grass productivity dynamics, which can provide useful insights into how these dynamics change over different spatial and temporal scales.

Author Contributions

Field work and experimental design was carried out by C. Moore, J. Beringer, L. Hutley and B. Evans. Data analysis was primarily carried out by C. Moore, with supplementary analysis

from J. Beringer (DINGO) and I. McHugh (error estimation). The manuscript was prepared by C. Moore with contributions from all co-authors.

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Table 1: List of instrumentation installed on the ecosystem and understory flux towers at the Howard Springs OzFlux site; where 'u' is the along wind component, 'v' is the across wind component and 'w' is the vertical wind component of wind velocity in 3-dimensional space, $K\downarrow$ and $L\downarrow$ refer to incoming and $K\uparrow$ and $L\uparrow$ refer to outgoing shortwave and longwave radiation, respectively.

Instrument	Make	Model	Description
Main Tower			
Open path CO_2, H_2O	Li-COR	LI-7500	23 m
Slow response CO2 concentration sensor	Vaisala	GMM220	23 m
Sonic Anemometer -wind velocities (u,v,w) -sonic temperature	Campbell Scientific	CSAT-3	23 m
Solar radiation ($K\uparrow$,$K\downarrow$, $L\uparrow$, $L\downarrow$)	Kipp and Zonen	CNR4	23 m
Solar net radiation	Kipp and Zonen	NR-Lite	23 m
Solar direct/diffuse	DeltaT Devices	SPN1	23 m
Atmospheric Pressure	Li-COR	LI-7500	23 m
Soil heat flux (4 replicates)	REBS	HFT3	-8 cm
Soil moisture	Campbell Scientific	CS616	-10 cm to -140 cm
Soil Temperature	Campbell Scientific	TCAV	-8 cm
Temperature and Relative Humidity	Vaisala	HMP45A	2 m, 23 m
Rain Gauge	Hydrological Services	TB3	Ground
Data Logger	Campbell Scientific	CR-3000	1.5 m
Power Supply -12V DC EC flux station	Kyocera	Solar panels (6) and battery bank	Ground
Camera	Vivotek	IP8362	23 m
PAR Quantum sensor	Li-COR	LI-191	2 @ 23 m
4-channel light sensor	Skye Instruments	SKR-1850	2 @ 23 m
Understory Tower			
Open path CO_2, H_2O	Li-COR	LI-7500	5 m
Sonic Anemometer -wind velocities (u,v,w) -sonic temperature	Campbell Scientific	CSAT-3	5 m
Solar radiation (All-wave)	Kipp and Zonen	NR-Lite	5 m
Temperature and Relative Humidity	Vaisala	HMP45C	5 m
Data Logger	Campbell Scientific	CR-3000	1.5 m

Table 2: Records of fire activity at the Howard Springs OzFlux site from years 2012 to 2014.

Year	**2012**	**2013**	**2014**
Julian day	Day 231 (19 Aug)	Day 158 (7 Jun)	Day 255 (12 Sep)
Mean intensity (kW m^{-1})	~2500	~1000	~2200

Table 3: Seasonal sums and annual mean (± SE) of net ecosystem productivity (NEP), respiration (R) and gross primary productivity (GPP) calculated for the savanna ecosystem, understory and overstory components at the Howard Springs OzFlux site, Northern Territory, Australia. Seasonal measurements are given in g C m^{-2} season^{-1} and annual measurements are given in g C m^{-2} y^{-1}.

		2012-2013 sums			2013-2014 sums			Mean (±SE)		
		Wet Season	Dry Season	Annual	Wet Season	Dry Season	Annual	Wet season	Dry season	Annual
Ecosystem	NEP	389.8	138.7	528.5	235.3	248.6	483.9	325.5 (±78)	193.7 (±55)	506.2 (±22)
	R	-1153.9	-664.8	-1818.7	-1102.7	-600.5	-1703.1	-1128.3 (±26)	-632.6 (±33)	-1760.9 (±58)
	GPP	1543.6	803.5	2347.1	1337.9	849.1	2187.0	1440.8 (±103)	826.3 (±23)	2267.1 (±80)
Understory	NEP	-376.9	-332.4	-709.3	-413.1	-322.6	-735.7	-395.0 (±18)	-327.5 (±5)	-722.5 (±14)
	R	-1004.5	-456.8	-1461.3	-923.9	-501.2	-1425.1	-964.2 (±40)	-479.0 (±22)	-1443.2 (±18)
	GPP	627.6	124.4	752.0	510.8	178.6	689.4	569.2 (±59)	151.5 (±28)	720.7 (±18)
Overstory	R	-149.4	-208.0	-357.4	-163.7	-99.3	-263.0	-156.5 (±08)	-153.7 (±55)	-317.7 (±47)
	GPP	916.0	679.1	1595.1	705.3	670.5	1375.9	810.7 (±106)	674.8 (±5)	1546.4 (±110)

		~~2012-2013 sums~~			~~2013-2014 sums~~			~~Mean (±SE)~~		
		~~Wet Season~~	~~Dry Season~~	~~Annual~~	~~Wet Season~~	~~Dry Season~~	~~Annual~~	~~Wet season~~	~~Dry season~~	~~Annual~~
~~Ecosystem~~	~~NEP~~	~~389.8~~	~~138.7~~	~~528.5~~	~~235.3~~	~~248.6~~	~~483.9~~	~~325.5 (±78)~~	~~193.7 (±55)~~	~~506.2 (±22)~~
	~~R~~	~~-1153.9~~	~~-664.8~~	~~-1818.7~~	~~-1102.7~~	~~-600.5~~	~~-1703.1~~	~~-1128.3 (±26)~~	~~-632.6 (±33)~~	~~-1760.9 (±58)~~
	~~GPP~~	~~1543.6~~	~~803.5~~	~~2347.1~~	~~1337.9~~	~~849.1~~	~~2187.0~~	~~1440.8 (±103)~~	~~826.3 (±23)~~	~~2267.1 (±80)~~
~~Understory~~	~~NEP~~	~~-376.9~~	~~-332.4~~	~~-709.3~~	~~-413.1~~	~~-322.6~~	~~-735.7~~	~~-395.0 (±18)~~	~~-327.5 (±5)~~	~~-722.5 (±14)~~
	~~R~~	~~-1004.5~~	~~-456.8~~	~~-1461.3~~	~~-923.9~~	~~-501.2~~	~~-1425.1~~	~~-964.2 (±40)~~	~~-479.0 (±22)~~	~~-1443.2 (±18)~~
	~~GPP~~	~~627.6~~	~~124.4~~	~~752.0~~	~~510.8~~	~~178.6~~	~~689.4~~	~~569.2 (±59)~~	~~151.5 (±28)~~	~~720.7 (±18)~~
~~Overstory~~	~~R~~	~~-149.4~~	~~-208.0~~	~~-357.4~~	~~-163.7~~	~~-99.3~~	~~-263.0~~	~~-156.5 (±08)~~	~~-153.7 (±55)~~	~~-317.7 (±47)~~
	~~GPP~~	~~916.0~~	~~679.1~~	~~1595.1~~	~~705.3~~	~~670.5~~	~~1375.9~~	~~810.7 (±106)~~	~~674.8 (±5)~~	~~1546.4 (±110)~~

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Table 4: Error estimates for net ecosystem exchange for the ecosystem and understory flux towers at Howard Springs OzFlux site, Northern Territory, Australia. Estimates are given for each year (2012-2014) and are presented as day (D), night (N) and total (T) error estimates in $g\ C\ m^{-2}\ t^{-1}$, where *t* is day, night or year.

		Available & Percentage (n, %) observations			**Model error**		**Random error**		**Combined error**
	Year	**D**	**N**	**T**	**D**	**N**	**D**	**N**	**T**
Ecosystem	**2012**	**2524, 87.2**	**404, 14.7**	**2928, 52**	**6.1**	**9.4**	**7.7**	**5.6**	**14.7**
	2013	**7657, 87.9**	**1653, 18.8**	**9310, 53.1**	**17.1**	**14.3**	**12.9**	**8.9**	**27.3**
	2014	**6121, 90.2**	**868, 12.4**	**6989, 50.7**	**12.0**	**11.7**	**11.6**	**7.5**	**21.7**
Understory	**2012**	**1786, 94**	**428, 23.2**	**2214, 59.2**	**1.4**	**7.7**	**4.0**	**5.9**	**10.6**
	2013	**7744, 91.9**	**2541, 28.2**	**10285, 59**	**8.4**	**29.7**	**8.4**	**10.5**	**33.6**
	2014	**6067, 92.7**	**2025, 28.2**	**8092, 58.9**	**4.4**	**30.8**	**7.4**	**9.0**	**33.2**

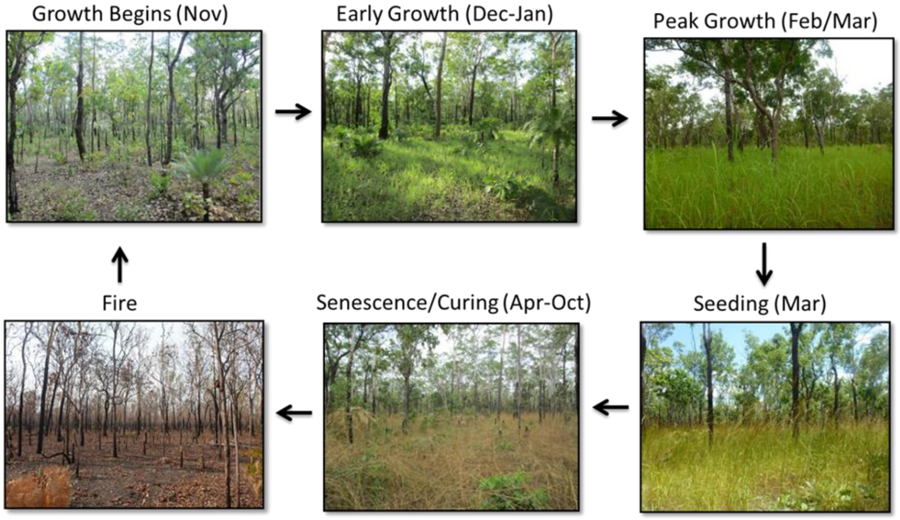

Figure 1: The variability in understory vegetation at Howard Springs OzFlux site, Northern Territory, Australia. The months from late October to early November are when growth in the understory begins, which continues on through the wet season until the end of March and start of April, when the understory grasses senesce and cure. The understory remains dry throughout the dry season months unless fire removes dry biomass.

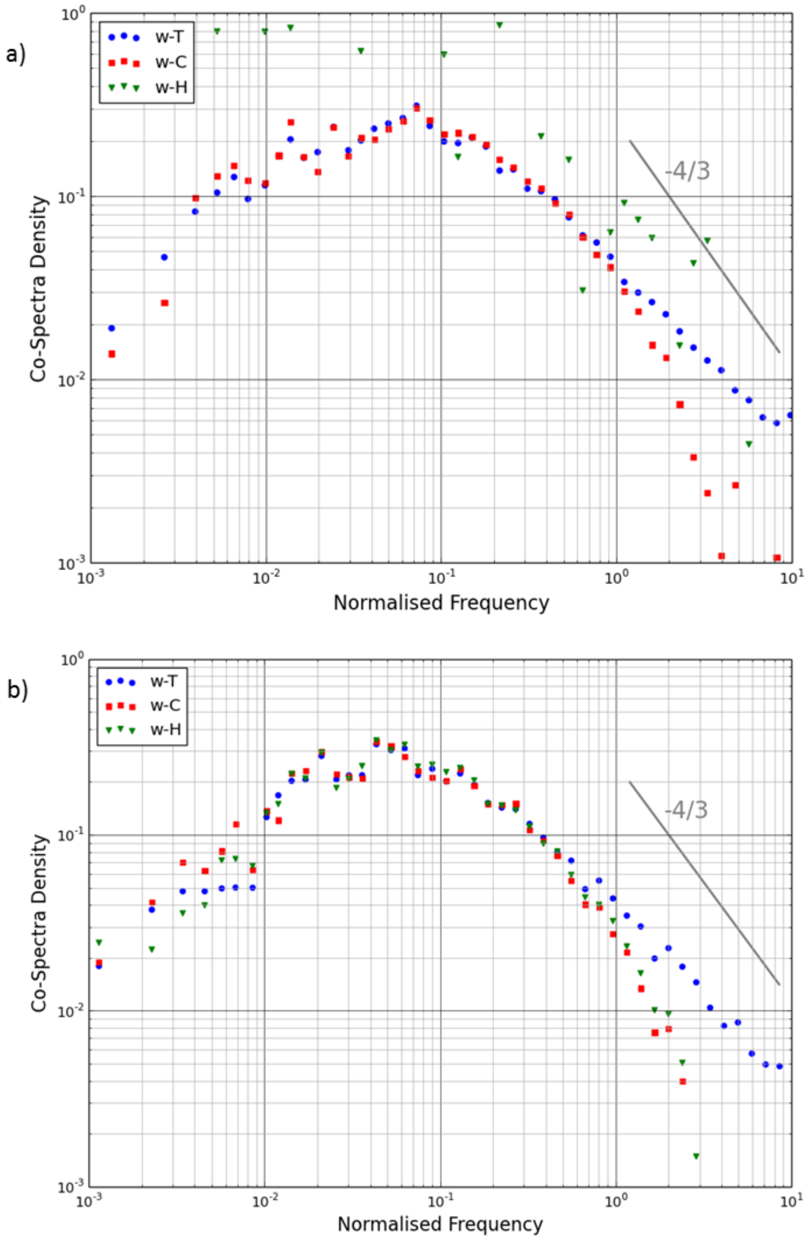

Figure 2: Co-spectra plot of vertical wind (w) against fluxes of carbon (w-C), water (w-H) and energy (w-T) for Howard Springs understory tower for the a) dry season and b) wet season. Co-spectra are grouped into 50 exponentially spaced frequency bins and represent times from 1200 to 1400, which are averaged over five consecutive days without rainfall for each season.

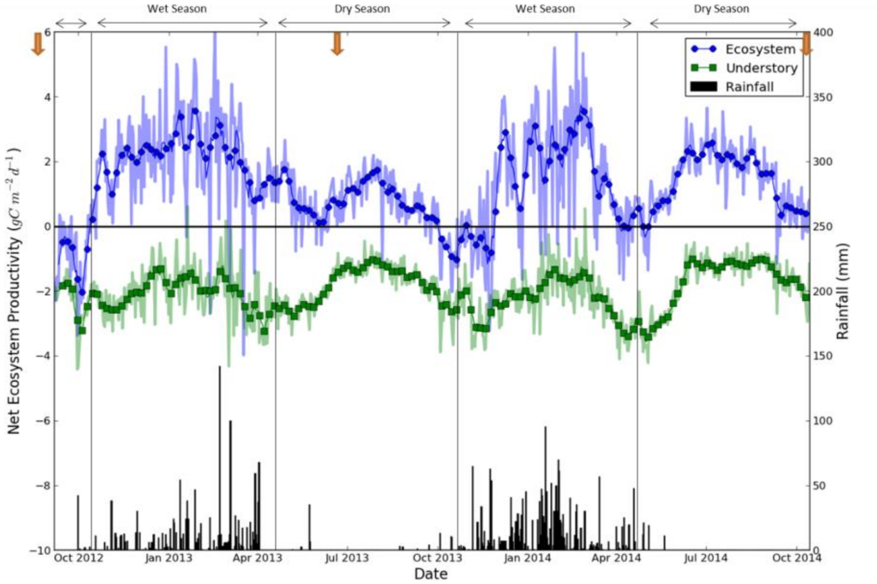

Figure 3: Net Ecosystem Productivity (NEP) for savanna ecosystem (23 m tower) and understory (5 m tower) components at the Howard Springs OzFlux site, Northern Territory, Australia from September 2012 to October 2014. Data shown are daily NEP totals with a 10-day running mean to aid visualisation. Orange arrows represent the timing of fire events (for fire intensity see Table 2). Positive fluxes indicate a net sink of carbon to the savanna whereas negative fluxes are a net source of carbon to the atmosphere. Rainfall is also included as daily totals.

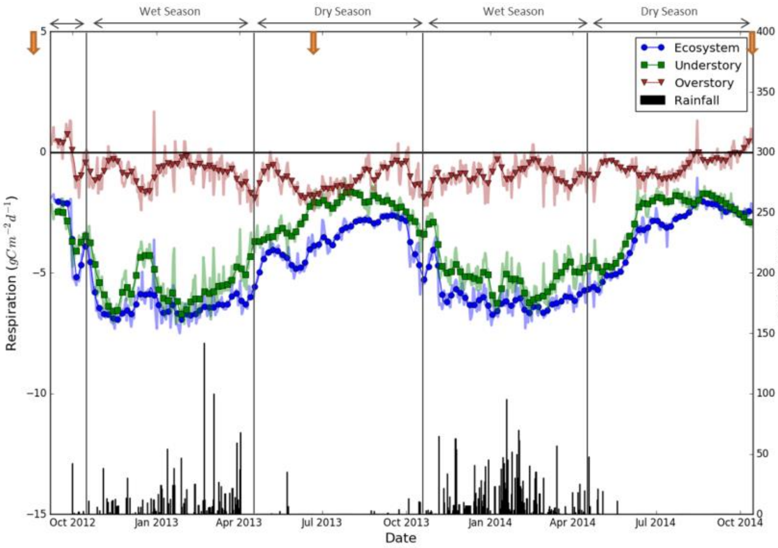

Figure 4: Respiration (R) for savanna ecosystem (23 m tower), understory (5 m tower) and overstory (difference between 23 m and 5 m towers) components at the Howard Springs OzFlux site, Northern Territory, Australia from September 2012 to October 2014. Data shown are daily R totals with a 10-day running mean to aid visualisation. Orange arrows represent the timing of fire events. Positive fluxes indicate a net sink of carbon to the savanna whereas negative fluxes are a net source of carbon to the atmosphere. Rainfall is also included as daily totals.

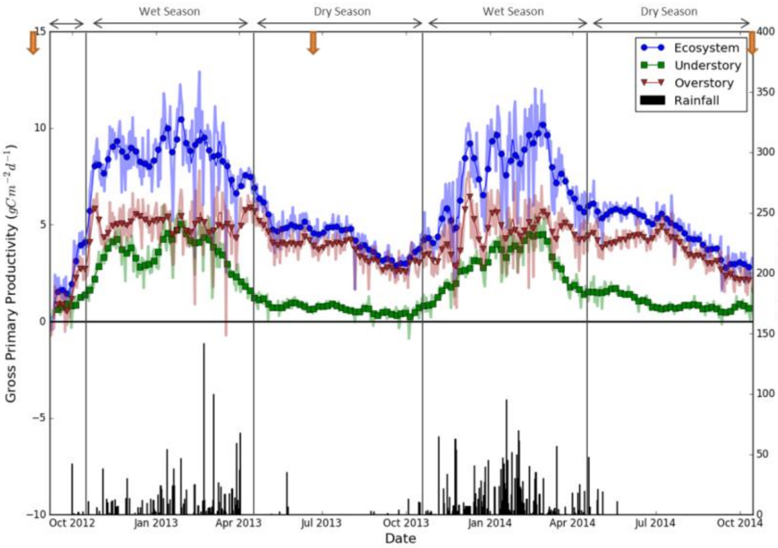

Figure 5: Gross Primary Productivity (GPP) for savanna ecosystem (23 m tower), understory (5 m tower) and overstory (difference between 23 m and 5 m towers) components at the Howard Springs OzFlux site, Northern Territory, Australia from September 2012 to October 2014. Data shown are daily GPP totals with a 10-day running mean to aid visualisation. Orange arrows represent the timing of fire events. Positive fluxes indicate a net sink of carbon to the savanna whereas negative fluxes are a net source of carbon to the atmosphere. Rainfall is also included as daily totals.

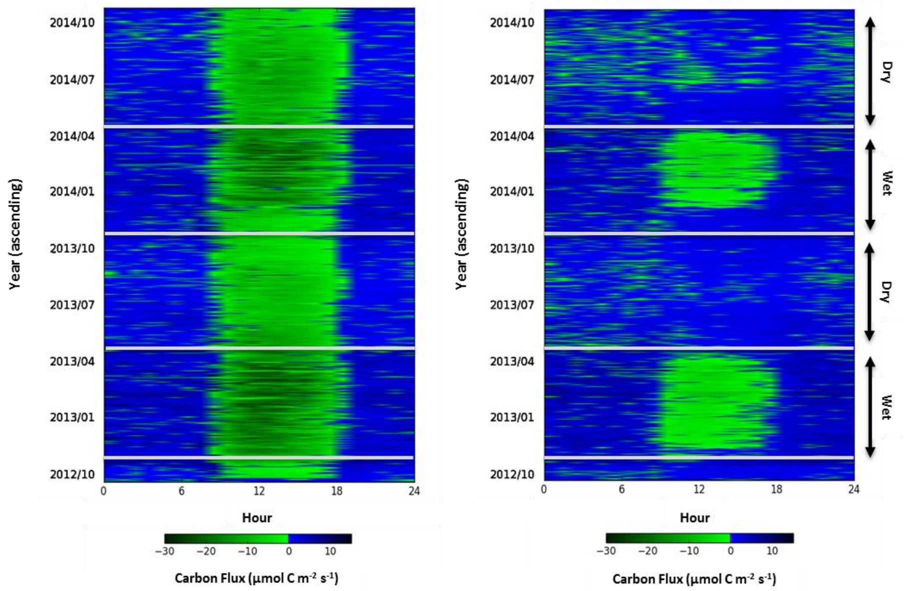

Figure 6: Diurnal (x-axis) fingerprint plot of NEE from the savanna a) ecosystem (23 m tower) and b) understory (5 m tower). Measurements shown are for 'wet' and 'dry' seasons from September 2012 to October 2014 (y-axis) at the Howard Springs OzFlux site, Northern Territory, Australia. Negative NEE represents the uptake of carbon by the savanna, whereas positive NEE represents the loss of carbon from the savanna.

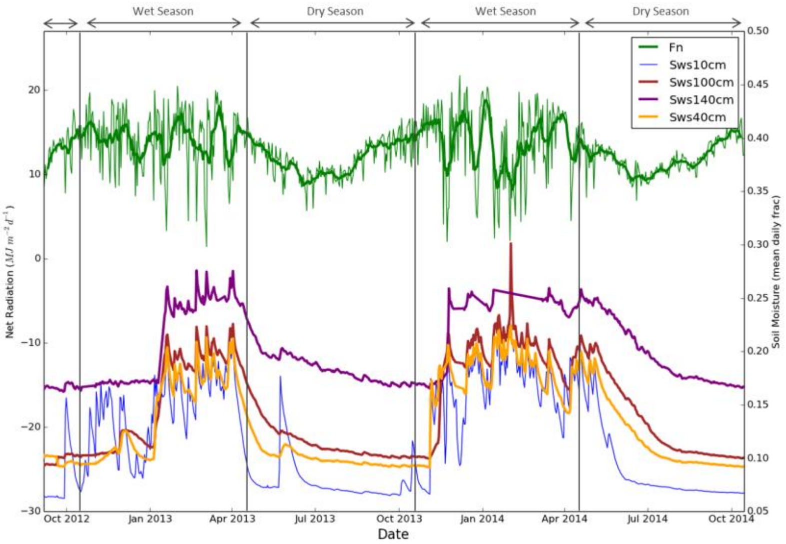

Figure 7: Daily variability in radiation (Fn) and soil moisture (Sws) at the Howard Springs tropical savanna site, Northern Territory, Australia from September 2012 to October 2014. Mean daily Fn is shown with a 10-day running mean (green) to aid in visualisation and daily mean variability in Sws fraction are shown for 10cm (blue), 40cm (orange), 100cm (brown) and 140cm (purple) depths.